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Studies of the Response of the Latham Raspberry to Pruning Treatment

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I. SOME EFFECTS OF PRUNING UPON GROWTH OF THE LATHAM RASPBERRY

W. G. Brierley

INTRODUCTION

A series of related investigations dealing with the growth of the Latham raspberry and its response to pruning treatment has been under way at the Minnesota Experiment Station for several years. Data were presented in an earlier publication (4) relative to the effects of height of pruning upon the size of berries and yield. The effects of height or severity of pruning upon growth and the food substances within the cane are dealt with in this bulletin. Reports have been made upon other phases of this series of studies, principally relating to cane structure, growth, and transpiration. These other studies of plant performance are referred to only when they appear to be related to the effects of pruning.

For the studies herein reported, the same plots were used in 1928 that were used for the fruiting studies in that year. The field was located at the University of Minnesota Fruit Breeding Farm and the plants were four years old. Additional work relating to the growth response following pruning treatment was carried on during 1933 in another field of the Latham variety growing at the Fruit Breeding Farm and maintained in accordance with the staked hill system of training.

REVIEW OF PREVIOUS WORK

Within recent years much attention has been given by horticultural workers to the study of the effects of pruning upon the fruiting performance of the red raspberry. The relation of the distribution of the winter buds to fruiting performance and the effects of pruning upon subsequent growth have also been noted. MacDaniels (13) in his studies of fruit bud formation in the raspberry observed that severe pruning tended to force a larger proportion of the basal buds into growth. He also reported that in the Herbert variety the new growth was greatly stimulated by severe pruning. Chandler (6) found that when canes were shortened considerably, longer flower-bearing shoots were produced. Johnston and Loree (10) noted that severe pruning reduced yield in the Cuthbert variety in Michigan. The location of the bud on the cane was found to affect the yield of the shoot subsequently produced, shoots from the basal and upper regions of the canes being poorer producers than

those from the central regions. Vigorous canes of large diameter produced the highest yields. Shoemaker (14), studying the response of the King variety in Ohio, also noted that yields increased as cane diameter and height increased. Lott (11) observed a similar relation of cane diameter to yield in the Cuthbert, Newman, and Latham varieties grown in Colorado. He noted that bud distribution was more uniform on the Latham canes than on the other varieties and that canes pruned to a height of five feet yielded more than those pruned to four feet. He noted further that there was no significant difference between the pruning treatments with regard to the vigor of the fruiting shoots.

Brierley (4) studied the effect of height of pruning upon the size of berries and total yield in the Latham variety in Minnesota and reported that the longer canes produced the larger yields when factors such as winter injury or drouth did not interfere. In this study it was also noted that the fruiting laterals seemed to increase in vigor as pruning increased in severity and that short canes tended to increase in height proportionately more than long canes because of the greater average length of the fruiting laterals. The present, more detailed studies indicate that one of the effects of severe pruning may be to reduce vigor, altho the opposite effect is suggested by observations in the field, where the effects of pruning are more apparent in average length of fruiting laterals than in the actual length of these shoots.

EFFECT OF SEVERITY OF PRUNING ON THE DEVELOPMENT OF VIGOROUS SHOOTS AT THE BASE OF OLD CANES

Observations of vigorous plants in the field have indicated that the Latham variety may be expected to develop an occasional new cane or exceptionally vigorous fruiting lateral within a few centimeters of the base of the canes. Figure 1 illustrates these two types of growth. The tendency to produce these vigorous shoots was increased slightly in the canes pruned to 36 inches and more so in canes pruned to 15 inches. This effect has been noted in the Herbert variety by MacDaniels (13), who suggests that the performance of these shoots reflects the stage of differentiation reached in the buds in the fall.

The production of these vigorous shoots has little effect upon field production. The fruiting shoots are so few that they add little to the total yield and do not extend the picking season materially. The few new canes produced apparently have no unusual value. They make useful canes in the hill system of planting as they arise within the confines of the hill. In the unsupported hedge row such canes are not likely to be as valuable as new canes arising from below ground, as they are sub-

ject to breakage at the point of union with the old cane. Fruiting laterals in such cases frequently grew to a length of 100 cm. or more. When the shoots developed into new canes they produced apparently normal growths, ranging from 150 to 200 cm. in height.

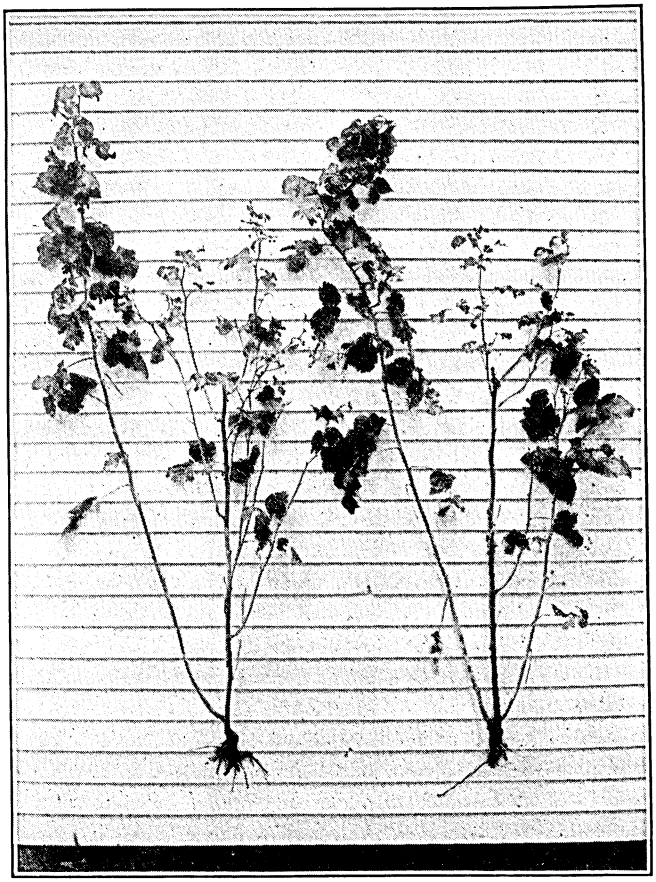

Fig. 1. Vigorous New Growth at Base of Old Canes
Left, new cane 68 inches long. Right, new cane 66 inches long and fruiting lateral 42 inches long. Both old canes pruned to 36 inches in early spring. The cane on the right was weakened by winter injury.

THE BEHAVIOR OF LATERAL SHOOTS ARISING FROM THE SAME NODE

Out of 6,140 nodes examined in 1928 there were 157, or 2.6 per cent, at which two laterals were produced. There were also a few nodes at which three laterals were developed. Canes pruned to 15 or 36 inches, or canes severely winter-injured at the tips, produced more of these twin laterals than normal canes pruned to 60 inches.

Table 1
Fruiting Behavior of Twin Laterals

Class	Behavior	Number
1	Both dead	3
2	Dead + non-fruiting	7
3	Dead + fruiting	18
4	Both non-fruiting	16
5	Non-fruiting + fruiting	55
6	Both fruiting	58

Table 1 shows the frequency of the various types of behavior of these laterals. As disease apparently caused the death of one or both laterals, as noted in the first three classes in the table, it may also have contributed to the low vigor of those which grew but did not fruit. These figures indicate that failure of one or both laterals to grow or fruit was more common than for both to fruit. Also, in most cases, both of the twin laterals were shorter than solitary ones nearby on the same canes. In the cases in which disease was not a factor it appears likely that the food reserves available in the old cane usually were not sufficient for the development of normal vigor. Also it is possible, on account of the more or less disorganized arrangement of the xylem at the point of shoot insertion, that water conduction was not adequate for the normal development of twin shoots.

The studies conducted in 1933 afforded an opportunity to compare the vigor of twin laterals with that of the usual solitary ones, and also to note the effect of severity of pruning upon the production of twin laterals. These data are presented in Table 2. From a study of this table it is clear that twin laterals were produced infrequently, occurring at only 1.5 per cent of the nodes under all pruning treatments. As pruning increased in severity, the percentage of twin laterals increased. On canes pruned to a height of five feet the percentage was negligible, but on the canes pruned to a height of one foot the percentage increased markedly, indicating that severe pruning tends to cause more of the weaker collateral buds to develop.

Altho the total number of cases in which the twin laterals were produced is small, the tabulation of the data shows that in no case was the vigor of the twin laterals observed to be greater than that of neighboring solitary ones. In only two cases was the vigor of these twins judged to be equal to the vigor of adjacent solitary laterals. In 19 cases one of the twins was noticeably weaker and in 13 cases both were weaker than the nearby solitary laterals. These observations are in close agreement with those of the earlier study.

No data were obtained relative to the frequency of this tendency for the Latham raspberry to produce collateral buds, but these observations

indicate that this behavior is not infrequent. It appears likely that the majority of nodes produce only one lateral shoot because of the suppression of the weaker buds, as in the grape, or because of disease.

Table 2

Relation of Vigor of Twin Laterals to Vigor of Adjacent Laterals and the Effect of Severity of Pruning upon This Behavior

Cane height	Both weaker	One weaker	Both as vigorous	Total	Total number nodes	Per cent nodes
1 foot	4	6	1	11	183	6.0
2 feet	3	5	0	8	376	2.1
3 feet	2	6	0	8	473	1.7
4 feet	3	2	0	5	500	1.0
5 feet	1	0	1	2	721	.03
Total	13	19	2	34	2,253	1.5

THE EFFECT OF SEVERITY OF PRUNING UPON THE NUMBER OF FRUITING LATERALS PRODUCED AT SUCCESSIVE HEIGHTS ON THE CANE

No detailed studies were made of the number of buds at successive heights on the canes, or of the effect of pruning upon the percentage of buds developing. Johnston and Loree (10) found that on canes of the Cuthbert variety many buds were winter-killed or remained dormant, and that other buds "produced weak shoots that later dried up." The latter part of this statement suggests the possibility that diseases may have prevented normal development of these shoots. Lott (11) found, in general, that the number of canes per hill had a greater effect upon bud performance than pruning the canes to four as compared to five feet in height. He also observed that the bud distribution is more uniform on the canes of the Latham variety than on the other varieties he studied.

In these studies observations were made relative to the number of fruiting laterals produced at successive heights on canes pruned to 15-, 36-, and 60-inch heights. These data are presented in Table 3. Because of the variability of the plots and the obvious effects of diseases, such as spur blight, no statistical treatment of these data was attempted. The table indicates the possibility that severe pruning to a height of 15 inches was effective in forcing more basal buds into growth. This is in agreement with the work of MacDaniels (13). The data also indicate that there may be a stimulation of bud development in the region of the cane adjacent to the point at which the cut is made in pruning. This wound stimulus is apparent in the canes pruned to a height of 36 inches and probably was effective in the canes pruned to 15 inches, altho in this case the equivalent number of shoots which must be used for comparison is of doubtful value.

The data presented in Table 3 also support the evidence obtained in the field to the effect that the upper portions of the canes were more or less affected by winter injury following delayed maturity. Fewer buds pushed into growth than were found at corresponding heights in the studies conducted during 1933. As the canes used in the later study were obviously well matured and uninjured, the number of fruiting laterals produced is considered representative of the variety and its response under local conditions.

Table 3

Effect of Severity of Pruning upon the Number of Fruiting Laterals at Successive Heights on the Cane, 1928

Position on cane	Length of cane in inches	Number canes	Average number fruiting laterals
First foot	15	218	2.4
	36	232	2.1
	60	239	1.4
Second foot	15	218	.9 (3.4)*
	36	232	2.1
	60	239	2.0
Third foot	36	232	3.3
	60	239	1.8
Fourth foot	60	239	2.4
Fifth foot	60	239	3.1

* Equivalent number per foot of cane.

For the studies conducted during 1933, hills of normal vigor were selected at random in the fruiting field. Six to ten hills were pruned at each height from one to five feet. The pruning was done on April 14 while the canes were still dormant. The data relating to the number and length of the fruiting laterals were recorded on July 3 at the time the first fruits ripened. As Brierley (5) has shown that elongation of laterals ceases with the development of the terminal berry, this time for recording the data was selected to avoid losses resulting from breakage in picking. The data relating to the number of laterals at a given height on the cane are presented in Table 5 and Figure 2.

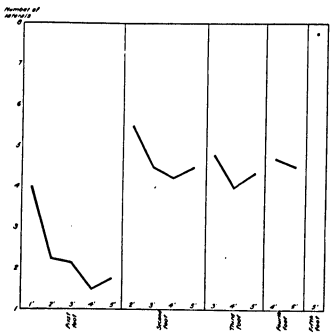

Fig. 2. Effect of severity of pruning upon the number of laterals produced at successive heights

In this study increasing severity of pruning seems to have stimulated the development of a larger number of fruiting laterals, not only in the first foot of the canes but in all other heights as well. The differences in the number of laterals are not as great in the upper portions of the canes, but the trend is apparent.

Whether this increase in the number of fruiting shoots is due to the pruning treatment or to a relative increase in the water supply of the more severely pruned canes has not been determined, but it is apparent that the increase in the amount of water available per foot of cane may have contributed to this result. Altho it has been found difficult to obtain satisfactory uniformity in the canes in a raspberry field, the canes in each pruning treatment obviously were comparable to those in any other treatment as to bud development, maturity, and the complement of stored foods. The observed increase in the number of shoots at a given height of cane cannot, therefore, be attributed to differences existing during the development and maturing of the canes but must be due to some stimulus related to pruning or to a change in the water relations of the canes, brought about by pruning.

LENGTH OF FRUITING LATERALS AS AFFECTED BY SEVERITY OF PRUNING AND POSITION ON THE CANE

A casual comparison in the field of the fruiting laterals borne by canes pruned to different heights may lead to the conclusion that severe pruning tends to stimulate these fruiting shoots into more vigorous growth. Such conclusions are frequently found in discussions of the effects of pruning in the raspberry. Lott (11), however, found that moderate pruning of the raspberry did not result in a significant increase in shoot vigor. With other fruits, numerous investigations have shown clearly that severe pruning in general tends to have a dwarfing effect upon the plant as a whole and in some cases reduces the vigor or length of the shoot growth which follows such treatment.

Studies of the effect of pruning upon the growth of fruiting laterals in the Latham variety were carried on in 1928 in plots pruned to 15, 36, and 60 inches, respectively. The results of these studies are presented in Table 4.

The data show that the laterals decline in length towards the tips in a fairly regular manner and that the differences in length between the various heights are statistically significant for any pruning treatment. This growth relationship has been noted previously by Johnston and Loree (10) in their studies of the Cuthbert variety, and it is a fact well-known to raspberry growers. Apparently this behavior is characteristic of the species and the pruning treatment does not materially affect it.

In the lower two feet of the canes there was a marked tendency for the laterals to be shorter as the pruning treatment became more severe. The growth produced on the canes pruned to 15 inches was shorter than that produced on either the 36- or 60-inch canes. In the first foot of

the canes these differences in length of the laterals are statistically significant. In the second foot, however, the difference between the growth on the 15-inch canes and that on the 36-inch canes was not significant, but the trend was toward shorter growth on the more severely pruned canes.

Table 4

Length of Fruiting Laterals as Affected by Height of Pruning and Position on the Cane

Position on cane	Pruning height, inches	Number laterals*	Average number laterals per cane	Mean length of laterals
				Cm. P.E.
First foot	15	191	3.0	55.7 ± .6
	36	110	1.7	62.3 ± 1.0
	60	133	2.3	64.9 ± 1.0
Second foot	15	66†	1.0	48.6 ± 1.0
	36	146	2.2	50.6 ± .7
	60	108	2.0	54.4 ± .9
Third foot	36	242	3.7	38.0 ± .5
	60	119	2.0	32.3 ± .7
Fourth foot	60	156	2.7	23.5 ± .6
Fifth foot	60	190	3.3	15.0 ± .7

* Laterals produced on 63 canes pruned to 15 inches, 66 canes pruned to 36 inches, and 57 canes pruned to 60 inches.

† Number of fruiting laterals at 12-15 inches.

Less difference in length of laterals was found between the canes pruned to 36 inches and those pruned to 60 inches. In the first foot of cane height the difference between these pruning treatments is not statistically significant but in the second foot the difference is significant. When all of the data for the first two feet of cane height are considered, it is apparent that in the Latham variety the lateral growth was shorter as pruning increased in severity.

In the third foot, the laterals produced on the canes pruned to 36 inches were longer than those produced on the 60-inch canes. This opposite growth response is believed to be due not to pruning, directly, but to the effect that removal of the upper portions of the cane had upon the water supply of the individual canes. In taller canes the competition for the available water obviously was more severe because of the greater number of laterals produced. It appears likely, from what is known relative to cane behavior, that in the upper portion of the canes water supply had a more marked effect upon growth than pruning treatment. In the lower portions of the canes, where the supply of water probably was adequate, the effects of the pruning treatments were not obscured.

The data suggest the possibility that severe pruning of the Latham raspberry may lead to a reduction in vigor, as in other fruit plants. The data also suggest that statements appearing in earlier publications, (4),

(6), (13), to the effect that severe pruning caused the development of longer fruiting laterals may have been based upon the *average* length which is definitely increased by the removal of the upper portion of the canes where the laterals usually are short.

In Table 5 and Figure 3, in which the data obtained in 1933 are presented, the trend towards shorter laterals on the more severely pruned canes is apparent for the first two feet of the canes, except in the case of the canes pruned to five feet. The trend, as in the earlier study, is in the opposite direction in the third and fourth feet of height. This latter effect is believed to result from the severe drouth and heat prevalent in 1933 and effective over a period of five weeks previous to July 3, when the measurements were made. This is considered further evidence in support of the statement that the performance of the raspberry cane as a whole is dependent more upon the moisture supply than upon pruning treatment.

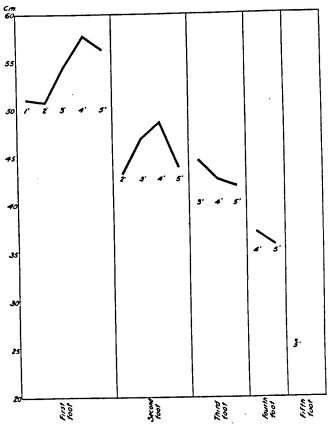

Fig. 3. Effect of severity of pruning upon the length of laterals produced at successive heights

Altho the differences in length between the laterals borne on the first two feet of the canes are not great enough to be statistically significant in all cases, the same trend appeared as in the earlier work. As will be

Table 5

Effect of Severity of Pruning on the Average Number and Mean Length of Fruiting Laterals at Successive Heights of the Canes, 1933

Position on cane	Total cane height, feet	Number canes	Average number laterals	Mean length of laterals
				Cm. P.E.
First foot	1	49	4.0	51.1 ± .8
	2	50	2.2	50.7 ± 1.2
	3	48	2.1	54.4 ± 1.4
	4	34	1.5	57.7 ± 1.8
	5	33	1.7	56.2 ± 1.8
Second foot	2	50	5.5	43.2 ± .6
	3	48	4.5	47.0 ± .8
	4	34	4.2	48.8 ± .8
	5	33	4.5	44.0 ± .9
Third foot	3	48	4.8	44.7 ± .6
	4	34	4.0	42.8 ± .7
	5	33	4.4	42.0 ± .8
Fourth foot	4	34	5.2	37.2 ± .6
	5	33	5.0	34.9 ± .7
Fifth foot	5	33	8.0	25.6 ± .5

pointed out later, this length relation may be more the indirect than the direct effect of severe pruning, as it may be brought about more by competition for food and water than by the pruning itself.

In Figure 4 the data are plotted with the successive heights of the canes as the abscissa and the mean length of the fruiting laterals as the ordinate. Plotted in this way it is apparent, as in the earlier studies, that the length of the fruiting laterals was influenced less by the pruning treatment than by position on the cane. The decline in the length of laterals from the base to the tips is regular enough to suggest a straight line relationship dependent upon cane height. It is apparent, however, that in the first foot of cane severe pruning tended to reduce the mean length of the laterals produced. In the second foot this trend is less definite, and in the third and fourth feet the effect was reversed so that longer laterals resulted from the more severe pruning treatments. It is believed that this effect was produced because in a dry season the longer canes had relatively less moisture available per foot of cane and this relative reduction in the moisture supply resulted in shorter growth in the upper portions of the canes.

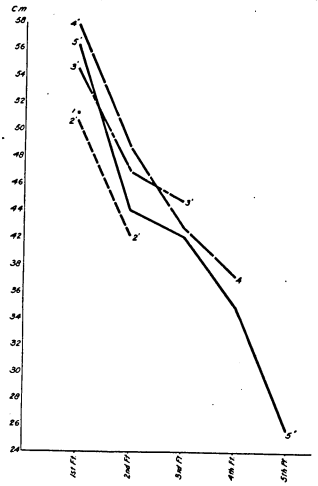

Fig. 4. Effects of severity of pruning and position of the cane upon the length of laterals produced at successive heights

CONCLUSIONS

From these studies it is apparent that there are two major effects of spring pruning or "tipping" upon the growth response. There is a tendency for severe pruning to result in the production of a greater number of laterals at a given height in the cane. There is also a less definite tendency for the mean length of these laterals to be less on the lower portions of the severely pruned canes. It is probable that these two effects are related, and that the shorter mean length of the laterals produced on the severely pruned canes is caused by the greater number produced and the more severe competition for stored foods and water.

It appears probable that the effects of pruning may be masked by the effect of other factors that affect growth. The variations that occur in the supply of foods and water, in the exposure to light, in the number of canes per hill, in the soil, and in the injuries produced by insects, diseases, or by wind storms affecting the connection with the root system, doubtless account for the variability in length of laterals that is apparent

at all heights of the canes. The introduction of the factor of pruning among these other variable factors affecting cane performance in the field obviously cannot be expected to lead to a clear-cut demonstration of the effects of pruning upon growth responses. To explain more fully the effects of pruning, it is evident that further study is needed on the subject of water intake and utilization in the cane and on the movement of food substances within the cane.

II. SOME EFFECTS OF PRUNING TREATMENT UPON THE FOOD SUBSTANCES IN THE FRUITING CANE

REVIEW OF PREVIOUS WORK

Apparently few studies have been made of the food substances occurring in raspberry canes or of the seasonal changes in, or movements of, these substances. Sablon (15) included the raspberry among the plants studied in relation to their food reserves. In the raspberry he traced the changes in the food substances of the roots, stems, and leaves. His data show for the canes in the second or fruiting year a rise in carbohydrates from February and March to the end of April during the development of foliage, flowers, and fruit, followed by a marked decline until October, but a considerable amount of residual carbohydrate material apparently remained at the end of the second year. His data (Table 27, p. 391) also show that the nitrogen content was higher in the second year from April to September than in the young canes. During the second summer he found that the reserves gradually diminished and the canes finally died. Lott (12) in his studies of the effect of certain types of hydrophilic colloids and of different field treatments upon hardiness in brambles in Missouri noted a general decrease during the winter in the total nitrogen in the bark, but because of the nature of the problem did not continue his studies into the fruiting season. Clements (8), studying the upward movement of inorganic solutes in plants, girdled some canes of the Cuthbert and Columbian raspberry varieties in April as the buds were swelling. These canes grew normally and fruited, but subsequent analyses showed a material increase in the relative amounts of nitrogen and ash in comparison with canes not girdled. No data were presented relating to carbohydrate changes, as he was studying only the inorganic solutes. Cherry (7) in his studies of the effect of chemical fertilizers upon growth and fruit production in black raspberries found that under all his fertilizer treatments the canes contained higher average amounts of carbohydrates in December than in July.

Altho a downward movement of carbohydrate and other food substances is known to occur in woody plants, little is known about this process in the red raspberry cane in the second year. As will be shown later, analyses indicate that in the dormant cane the proportionate amount of sugars increases from the base to the tips of the canes. Very little evidence is available to show whether these food materials are translocated downward for the use of fruiting laterals in the basal region, but possibly this does occur to some extent. Sablon (15) concluded that the high carbohydrate content he found in the canes in the spring of the second year resulted from translocation upward from the roots, as the reserves in the cane were being used in the formation of fruits, and in respiration. Bennett (2) and Clements (8) have noted the development of callus formation above girdled areas on fruiting canes, a fact which indicates that downward movement of foods was arrested by the girdle. Brierley (3) found that the phloem in the fruiting canes begins to break down about the height of the fruit ripening season. This seemingly would prevent downward movement of food substances at and after that time, but such movement might occur previous to the breakdown of the phloem.

Further studies of the movement of food substances in the raspberry cane are needed to explain fully the rôles of the new and old canes in the performance of the plant. The data relating to some of the food substances found in the dormant cane, the changes which take place during the fruiting season, and some effects brought about by pruning are presented herein as an approach toward the solution of the general problem.

PREPARATION OF MATERIALS, AND ANALYTIC PROCEDURE

Samples of canes for analysis were cut from each of the plots at the Fruit Breeding Farm in the late afternoon. Samples were taken at the several stages of cane development from the four plots of each pruning height. Duplicates of each of these were used in the various determinations. After the start of active growth, the canes were defoliated as they were removed from the plots and suitably protected against drying. The material so treated was kept in a cool storage cellar over night and then taken to the laboratories at University Farm, where it was prepared for analysis. The canes and laterals were cut with pruning shears into lengths of one-quarter to one-half inch. After thoroly mixing to insure uniformity of the samples, 6 to 10 grams were removed for the determination of moisture, organic nitrogen, and ash. This fraction was dried to constant weight at 102° C. for moisture determinations and the

residue ground to a fine powder for the determination of organic nitrogen and ash. Fifty gram portions of the samples were immediately preserved in Mason jars by boiling in 95 per cent alcohol to which approximately one gram of calcium carbonate had been added. After boiling for 30 minutes the jars were sealed and stored until the analyses could be made. Analyses were made in duplicate from each plot in each of the four series and the data presented are the averages of these eight determinations. As the data obtained from the analyses of the samples from the plots pruned to 15 and 60 inches showed in general only minor effects due to the pruning treatment, no analyses were made to determine the concentration of total sugars, reducing sugars, "starch" and amino nitrogen in the 36-inch canes after the blooming period.

The analytic procedure followed was essentially the same as that used by Hildreth (9) and Traub (16) for somewhat similar studies. Official methods of analysis of the Association of Official Agricultural Chemists (1) were used.

OCCURRENCE OF CERTAIN FOOD SUBSTANCES IN THE DORMANT CANES

A representative sample consisting of 25 dormant canes was taken from the field on March 27, 1928. The canes were cut from plants outside the plots in order to avoid too severe thinning in the plots themselves. The material was judged to be comparable to that in the plots. All buds were removed in the laboratory and preserved for analysis. The canes were cut at the heights of 15, 36, and 60 inches, thus dividing them into four sections, at heights similar to the pruning treatment in the plots. As the canes were approximately 72 to 78 inches in length, tip sections varying from 12 to 18 inches were obtained from the majority of the canes. Duplicate samples from the material from each of these four sections were analyzed and the results are presented in Table 6 and Figures 5 and 6. These data show an increase in the proportionate amount of dry matter from the basal region towards the tips of the canes. This apparently is due in part to the tendency of the less well matured tip region to lose some of its moisture content during the winter, and in part to the fact that the basal section, formed during the

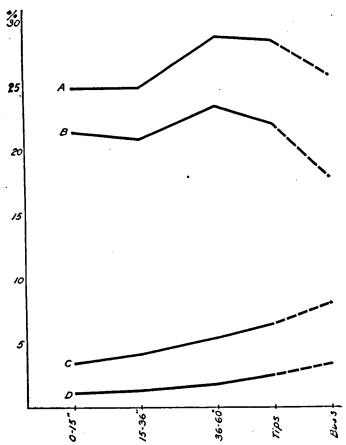

Fig. 5. Carbohydrate materials at successive heights in the dormant cane
A. Total carbohydrates. B. "Starch." C. Total sugars. D. Reducing sugars.

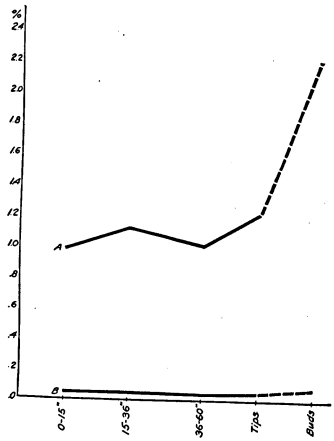

Fig. 6. Nitrogenous materials at successive heights in the dormant cane
A. Total nitrogen. B. Amino nitrogen.

period of rapid growth, contains more and larger vessels and the pith area is proportionately larger. It is obvious that such cells, usually without contents, may contribute to a somewhat lower dry weight. The percentage of dry matter was lowest in the buds where the dormant growing points and partially differentiated tissues would be expected to contain a relatively high percentage of moisture.

Reducing sugars and total sugars were found to increase in concentration towards the tips and were highest in the buds (Fig. 5). The relation of height in the cane to the concentration of "starch," the acid hydrolizable carbohydrates other than sugars, is not so regular. The region between 36 and 60 inches was found to have the highest concentration of these materials, but the concentration in the tip region was only a little less. That there was relatively less in the lower portions of the canes indicates that a part may have been used in the thickening of cell walls or that the simpler carbohydrates were translocated to the roots instead of being used in the formation of these more complex forms. That there was somewhat less in the tip region also may have been due to the late formation of this part of the canes and the shorter time available for

Table 6

Occurrence of Certain Food Substances in Dormant Canes at Successive Heights, Expressed in Percentage of Dry Weight Samples Collected March 27, 1928

	Region of cane				
	0-15 in.	15-36 in.	36-60 in.	Tips above 60 in.	Buds
	per cent	per cent	per cent	per cent	per cent
Moisture*	50.06	49.75	47.16	45.55	53.46
Dry matter*	49.94	50.25	52.84	54.45	46.54
Reducing sugars	1.22	1.27	1.78	2.55	3.27
Total sugars	3.48	4.10	5.36	6.45	8.12
"Starch"	21.48	20.88	23.45	22.05	17.73
Total reserve carbohydrates	24.96	24.98	28.81	28.50	25.85
Amino nitrogen	0.046	0.049	0.041	0.047	0.080
Total organic nitrogen	0.982	1.127	1.004	1.209	2.201
Amino nitrogen as per cent total nitrogen	4.69	4.24	4.15	3.95	3.61
Ash	1.30	1.36	1.47	1.86	6.36

* Expressed as per cent of green weight.

the formation of these more complex carbohydrates. Total reserve carbohydrates were found in somewhat greater concentration in the upper portions of the canes. As "starch" was relatively so large a fraction, it is obvious that the relation of height in the cane to concentration of total carbohydrates would be essentially the same as for the starch fraction.

The concentration of amino nitrogen (Fig. 6) was very small, and it varied only a little throughout the length of the canes. It was highest in the buds, as would be expected. The relative amounts of total organic nitrogen increased with height of cane except for an unexplainable drop at the 36- to 60-inch height, and was highest in the buds. As the percentage of amino nitrogen remained fairly uniform throughout the cane, it is obvious that the expression of the occurrence of this material in percentage of total nitrogen would show a decline with height of cane.

The percentage of ash was found to increase toward the tips of the canes and was much higher in the buds.

These data show the occurrence of these food substances per unit of dry weight. Altho the concentration of some of these substances increases toward the tips of the canes, there is much more wood and bark in the basal and central regions of normal canes than at the tips, and presumably there is in the lower parts of the canes a larger volume of the tissues concerned with food storage. For this reason the actual amount of the common food substances may be as large or larger toward the base of the canes as toward the tips, even tho the percentage increases toward the tips.

Whatever the relation may be between the actual amount of these substances and the concentration per unit of dry weight, it is apparent that the removal of the upper portions of the canes in pruning results in the loss of a considerable quantity of stored foods. If the tips must be removed because of winter injury or to obtain the proper length to enable the canes to remain erect under their load of foliage and fruit, it is obvious that the loss of stored foods is of secondary importance. But with uninjured canes, the best field management may involve a minimum of tipping and the supporting of the canes by stakes or wires in order to obtain the maximum economy of these food substances.

CHANGES IN THE MOISTURE CONTENT OF CANES AND FRUITING LATERALS DURING THE FRUITING SEASON

It has been noted in the study of the moisture content and dry weight of dormant canes that the dry weight increases slightly toward the tips, with a corresponding decrease in moisture content. Obviously pruning of the dormant canes cannot be expected to upset the moisture situation

in the canes themselves, altho severity of pruning does affect the relative amounts of soil water available per unit of cane. The data relating to the changes in the moisture content of the canes pruned at the three heights are presented in Table 7. The changes occurring in the 15-inch and 60-inch canes are also shown graphically in Figure 7. The percentage of moisture in the 15-inch canes on March 27 is in close agreement with that shown in Table 6. The moisture content of the 60-inch canes is not quite as low as might be expected with the upper portions of the canes, containing a lower percentage of moisture, included in the samples. Similarly the moisture percentage in the 36-inch canes is slightly higher than might be expected. As these percentages were derived in each case from duplicate samples from four plots, they may be considered to be representative of the material. These minor discrepancies, and others appearing later, may be attributed in part to the expected variability of the material and in part to the unavoidable delays involved in the handling and transporting of the samples.

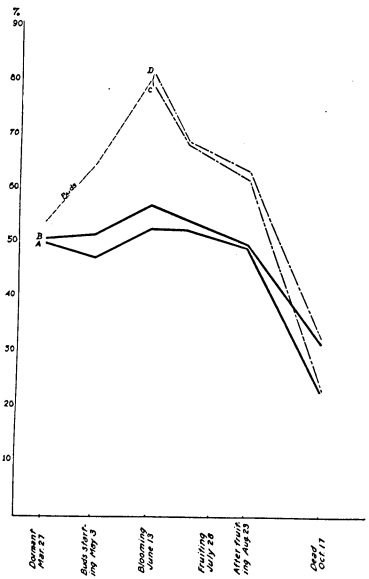

Fig. 7. Seasonal changes in moisture content
A. 60-inch canes. B. 15-inch canes.
C. Laterals from 60-inch canes.
D. Laterals from 15-inch canes.

Table 7

Changes in the Moisture Content of Canes and Fruiting Laterals During the Season

	March 27, dormant	May 3, buds starting	June 13, bloom	July 28, fruiting	Aug. 23, after fruiting	Oct. 17, dead
15-inch Canes	50.74	51.50	57.18	54.61	50.09	32.18
Laterals	....	....	81.05	68.53	63.37	33.21
36-inch Canes	52.40	48.78	54.71	53.28	50.89	33.35
Laterals	....	....	79.84	67.92	62.95	24.77
60-inch Canes	49.95	47.39	52.98	52.74	49.51	23.39
Laterals	....	....	78.72	67.96	61.67	23.68
Buds	53.46	64.74	....	....	....	....

At the time the buds began to grow, their moisture content increased materially. At the same time the moisture decreased slightly in the longer canes but increased slightly in the short canes. This indicates

that as the buds start, they draw on the moisture supply of the canes more rapidly than it is replaced in the taller canes.

At the time of blooming, the moisture content in all heights of pruning was higher than at any other time during the season. There was a slight decline at the height of the fruiting season and a somewhat more rapid decline after the fruit was all picked. From then until the canes died, they were failing and drying so it is to be expected that the moisture content of the dead canes would be low.

The moisture content of the fruiting laterals was noticeably higher than in the canes from the time of blooming until after fruiting, but when the canes died declined to about the same percentage as in the canes. The laterals are much less "woody" than the canes, and as they are even more temporary growths than the canes proper they may be expected to have a higher moisture content and, conversely, a lower dry weight.

Pruning apparently had little effect upon the moisture content of the canes and laterals. There was a slightly higher percentage of moisture in both the canes and laterals when the canes were pruned to 15 inches. This difference may be due to the fact that canes growing in the same soil have a similar supply of soil moisture available and that severe pruning tends to increase the relative amounts available for the shortened canes.

CHANGES IN THE PERCENTAGE OF TOTAL SUGARS

The percentage of total sugars in the canes was found to decline rapidly with growth of the buds and the development of flowers and fruit. The buds were high in sugar content which declined rapidly as growth began. Presumably much of this decline may be accounted for in rapid cell division and the development of fibers and other cells concerned with the supporting structure of the stem. At the time of blooming the laterals were found to have a relatively high percentage of total sugars. As this concentration was found at a time when the percentage in the canes themselves had declined markedly, it is apparent that sugars had been translocated from the canes to the laterals. It is probable, however, that a part of this accumulation of sugars was due to photosynthesis in the leaves borne by the laterals. There was a marked decline in the percentage of total sugars in the laterals between the time of bloom and the height of the fruiting season. Apparently this loss was due mainly to translocation to the fruit and to respiration, altho a small portion may have been converted into starch. These data are presented in Table 8 and Figure 8.

After the picking season, an increase in total sugars was noted in both canes and laterals. During this period the foliage remained in

Fig. 8. Seasonal changes in the percentage of total sugars
A. 60-inch canes. B. 15-inch canes.
C. Laterals from 60-inch canes.
D. Laterals from 15-inch canes.

fairly good condition and apparently continued to synthesize sugars which were translocated to the laterals and canes. In other woody stems in the later part of the growing season there is generally a translocation of these food substances downward into older portions of the stem and to the roots. That these substances increased in percentage in the old canes at this time is thought to be due at least in part to the breakdown of the phloem, which Brierley (3) has shown begins soon after the picking season. The general upward movement of sugars noted during the early stages of growth and as the fruit developed is in agreement with the work of Sablon (15). The increase in sugars after fruiting, at the time when the phloem is breaking down, indicates that the old canes do not contribute to the supply of sugars stored in the roots. It may be concluded from these data that the removal of the old canes after the crop is picked can have no effect upon the amount of sugars stored in the roots at that time.

Table 8

Changes in the Percentage of Total Sugars (as Glucose), Expressed in Percentage of Dry Weight

	March 27, dormant	May 3, buds starting	June 13, bloom	July 28, fruiting	Aug. 23, after fruiting	Oct. 17, dead
15-inch Canes	3.95	2.23	.98	.95	1.43	.43
Laterals	...	...	5.08	2.71	3.52	.62
36-inch Canes	4.27	2.16	...	...	...	...
Laterals	...	...	...	...	...	...
60 inch Canes	4.26	2.28	1.77	1.38	1.86	.47
Laterals	...	...	5.19	2.57	3.43	.67
Buds	8.12	4.06	...	...	...	...

In the dead canes a small residue of sugars was found. This may have been due to the presence of tannin or other reducing substances. The decline in sugars in both canes and laterals as the canes died is thought to be due partly to respiration and partly to conversion into other carbohydrates.

Severity of pruning apparently had little effect upon the behavior of the total sugars. To lessen the time required for these studies no

analyses were made to determine the percentage of sugar in the canes pruned to 36 inches after the time growth began. The tendency for the longer canes to contain a somewhat higher concentration of total sugars is thought to be due merely to the inclusion in the samples of the upper portions of the canes in which larger quantities of these substances are found (see Table 6 and Figure 5).

CHANGES IN THE PERCENTAGE OF REDUCING SUGARS

The changes in the percentage of reducing sugars throughout the fruiting season were found to follow a course similar to that of the total sugars. These data are presented in Table 9 and Figure 9. In the canes there was a steady decline from the highest concentration in the dormant canes until the picking season. In the laterals the decline was rapid from the time of blooming to the picking season. As in the case of the total sugars, this decline probably is due to the utilization of these substances in the growth of the laterals and in the development of the fruit.

As in the case of the total sugars, there was an increase in percentage after all the fruit had been picked, this increase occurring at the time of the observed breakdown in the phloem. This indicates that the old cane is unable to move these foods downward to the roots, and the sugars accumulate as a residue which is of no value to the root system or to the new canes. Apparently this increase in sugars is not of long duration as the foliage fails rapidly during late August and September. As the percentage found in the dead canes is low it is evident that the reducing sugars, like the total sugars, have been used in respiration or in other ways until only a small residue remains.

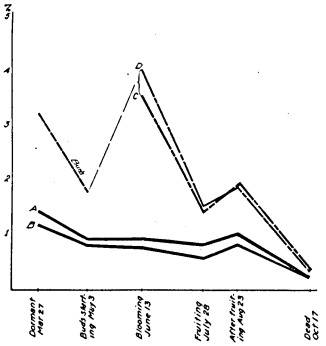

Fig. 9. Seasonal changes in the percentage of reducing sugars
A. 60-inch canes. B. 15-inch canes.
C. Laterals from 60-inch canes.
D. Laterals from 15-inch canes.

As in the case of the total sugars, severity of pruning appears to have had only a minor effect upon the reducing sugars. The 60-inch canes showed a slightly higher percentage throughout the season than was found in the 15-inch canes but this was probably because the upper portions of the canes were included in the samples of the 60-inch canes. These upper portions contain somewhat higher concentrations of sugars and thus tend to raise the percentages of the longer canes.

Table 9

Changes in the Percentage of Reducing Sugars, Expressed in Percentage of Dry Weight

	March 27, dormant	May 3, buds starting	June 13, bloom	July 28, fruiting	Aug. 23, after fruiting	Oct. 17, dead
15-inch Canes	1.20	0.84	0.80	0.61	0.86	0.24
Laterals	...	...	4.08	1.57	1.91	0.37
36-inch Canes	1.36	0.90	...	...	...	...
Laterals	...	...	...	...	...	...
60-inch Canes	1.47	0.96	0.97	0.86	1.07	0.25
Laterals	...	...	3.60	1.47	1.97	0.38
Buds	3.27	1.81	...	...	...	...

CHANGES IN THE PERCENTAGE OF "STARCH"

The percentage of starch, the acid hydrolyzable carbohydrates other than sugars (except cellulose), comprised much the larger fraction of the total carbohydrates found in the canes, and throughout the season was found to follow much the same order of seasonal changes as the sugars. The data obtained are presented in Table 10 and Figure 10. A slight increase was found in the canes at the time the buds were starting. This was followed by a decline until the time of blooming, the same period in which the sugars were found to decrease in percentage, and when the laterals were growing rapidly. Between blooming and the picking season the percentage in the 60-inch canes decreased slightly, while it increased slightly in the 15-inch canes. In the period following the picking season there was an increase in starch similar to the increase noted for sugars. This increase, probably due to the conversion of some sugar into starch, is without significance other than to support the conclusion that the breakdown of the phloem prevented the downward translocation of carbohydrate materials. In the dead canes the percentage of starch was found to have declined, but a fairly large residue remained.

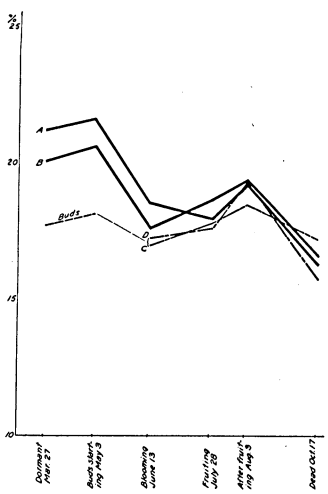

Fig. 10. Seasonal changes in the percentage of "starch," the acid hydrolyzable carbohydrates other than sugars
A. 60-inch canes. B. 15-inch canes.
C. Laterals from 60-inch canes.
D. Laterals from 15-inch canes.

This decline in percentage of starch, when considered in its relation to total sugars, is in agreement with the results of Sablon (15) except for the increase in both starch and sugars in the period following fruiting. These changes in the

starch and total sugars found in the 60-inch canes are shown graphically in Figure 11.

When the buds began growth, the percentage of starch was slightly higher than in the dormant buds. In the laterals there was a slight decline at the time of blooming, followed by a slight but fairly regular increase through the height of the fruiting season. In the dead laterals the percentage had declined at about the same rate as in the canes. Apparently a small part of the decline in total sugars between the time of blooming and the picking season may be due to the formation of starch. This slight increase in the percentage of starch from the blooming period until the time following fruiting probably is related to the decline in the phloem and associated with the increase in total sugars. The failure of the food transport mechanism apparently begins at a slightly earlier date in the laterals than in the canes proper.

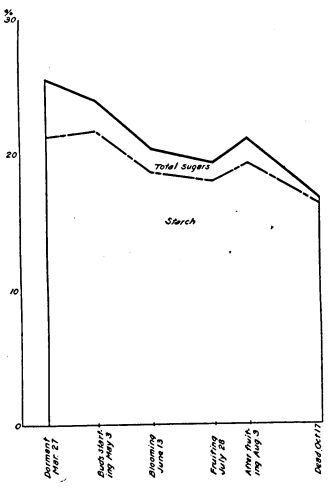

Fig. 11. Seasonal changes in the total reserve carbohydrates in 60-inch canes shown by superimposing the percentages of total sugars upon those for "starch"

As in the case of total sugars and reducing sugars, the degree of severity of pruning appeared to have little effect upon the amount of starch found in the canes.

Table 10

Changes in the Percentage of "Starch," the Acid Hydrolyzable, Carbohydrates Other Than Sugars, Expressed in Percentage of Dry Weight

	March 27, dormant	May 3, buds starting	June 13, bloom	July 28, fruiting	Aug. 23, after fruiting	Oct. 17, dead
15-inch Canes	20.08	20.66	17.66	18.71	19.42	16.65
Laterals	....	....	17.27	17.63	19.34	15.79
36-inch Canes	21.11	21.28	....	....	....	....
Laterals	....	....	....	....	....	....
60-inch Canes	21.23	21.69	18.59	17.99	19.26	16.30
Laterals	....	....	17.00	17.82	18.51	17.27
Buds	17.73	18.19	....	....	....	....

CHANGES IN THE PERCENTAGE OF TOTAL ORGANIC NITROGEN

The percentage of organic nitrogen, altho always relatively small, was found to be highest in the dormant canes and decreased more or less regularly throughout the season. The data presented in Table 11 indicate that pruning had little effect upon these materials, altho the percentages were as a rule somewhat greater in the longer canes.

The percentage of organic nitrogen was relatively high in the buds and in the laterals at the time of blooming. After this stage of growth there was little difference between the laterals and the canes. There was a slight increase in the percentage in the laterals in the period following fruiting. In the dead canes a drop in the percentage found in the laterals was accompanied by a slight increase in the canes. It is thought that this behavior was due to the breakdown of the phloem and the resulting effect upon the translocation of food materials.

As organic nitrogen usually is found in greater amounts in actively growing tissues, and as the old cane and fruiting laterals are obviously progressively senescent, the decline in percentage of these substances in the old cane and its laterals may be regarded as normal behavior.

Pruning appeared to have no appreciable effect upon the occurrence of organic nitrogen, except that in severe pruning the removal of the upper portions of the cane, in which the percentage was slightly higher, resulted in a slight decrease in this type of food material in the shorter canes.

Table 11

Changes in the Percentage of Total Organic Nitrogen, Expressed in Percentage of Dry Weight

	March 27, dormant	May 3, buds starting	June 13, bloom	July 28, fruiting	Aug. 23, after fruiting	Oct. 17, dead
15-inch Canes	0.980	0.900	0.697	0.612	0.528	0.629
Laterals	....	....	1.608	0.673	0.700	0.464
36-inch Canes	1.056	0.996	0.677	0.697	0.577	0.566
Laterals	....	....	0.927	0.715	0.740	0.538
60-inch Canes	1.052	1.014	0.689	0.728	0.634	0.655
Laterals	....	....	1.193	0.763	0.782	0.520
Buds	2.201	....	....	....	....	....

CHANGES IN THE PERCENTAGE OF AMINO NITROGEN

Amino nitrogen was formed in very small amounts in the canes. In the buds and laterals relatively larger amounts were found, but the quantities were small in comparison with other food substances. In Table 12 the data relating to the amount of amino nitrogen found at the

various stages of cane development are presented in percentage of the dry weight and in percentage of the total organic nitrogen. Except for a slight increase at the time the buds were starting to grow, there was a general decline in the percentage of amino nitrogen in the canes throughout the season. In the buds and laterals the percentage was highest at the time of blooming. As the blossoms open at about the time active growth ceases, it is likely that larger amounts may occur in the actively growing laterals. From the time of blooming until the death of the laterals there was a marked decline in amino nitrogen. As the old cane and laterals are in a senile condition, at least after blooming, and as amino nitrogen usually is associated with active growth, a decrease in the percentage of amino nitrogen as the season advanced might be expected.

Pruning apparently had no material effect upon the amounts of amino nitrogen found in the canes or laterals. In the data relating to the occurrence and concentration of food substances in dormant canes (Fig. 6) it has been shown that the percentage of amino nitrogen is about the same at all heights in the cane. Also, the dry weight and the amount of total organic nitrogen were found to increase with height in the cane. Apparently the effect of severe pruning in removing a greater portion of the upper part of the canes is merely to reduce somewhat the amounts of dry materials and total organic nitrogen and thus indirectly to affect the percentage of amino nitrogen.

CHANGES IN THE ASH CONTENT OF FRUITING CANES AND LATERALS

The data relating to the ash content of the canes and fruiting laterals are presented in Table 13. The percentage of ash in the canes varied little, either with the progress of the season or as affected by severity of pruning. The slightly larger percentage found in the dead canes may be due to a downward movement from the laterals or to the slight accumulation of these substances carried into the cane in the transpiration stream after the fruiting season.

In the buds the percentage of ash was relatively high, but decreased markedly as growth began. This possibly was due to the development of fibrous material that greatly affected the total dry weight and thus relatively reduced the percentage of ash. The highest percentage in the laterals occurred at the time of blooming. There was a rapid decrease between then and picking time, which was probably due to the movement of these materials into the berries. Through the remainder of the season the decline was not great and, as pointed out above, may have been due to a downward movement into the canes.

Table 12

Changes in the Percentage of Amino Nitrogen, Expressed as Percentage of Dry Weight and as Percentage of Total Nitrogen

	March 27, dormant		May 3, buds starting		June 13, bloom		July 28, fruiting		Aug. 23, after fruiting		Oct. 17, dead	
	Per cent of dry weight	Per cent of total nitrogen	Per cent of dry weight	Per cent of total nitrogen	Per cent of dry weight	Per cent of total nitrogen	Per cent of dry weight	Per cent of total nitrogen	Per cent of dry weight	Per cent of total nitrogen	Per cent of dry weight	Per cent of total nitrogen
15-inch Canes	.049	5.00	.055	6.11	.031	4.48	.024	3.92	.020	3.79	.013	2.09
Laterals	...	...	...	...	.239	14.86	.087	12.93	.055	7.86	.014	3.02
36-inch Canes	.041	3.91	.054	5.83	...	...	...	...	...	...	...	...
Laterals	...	...	...	...	...	...	...	...	...	...	...	...
60-inch Canes	.046	4.36	.049	4.83	.027	3.92	.019	2.61	.019	3.00	.013	1.98
Laterals	...	...	...	...	.213	17.85	.054	7.08	.054	6.91	.020	3.85
Buds	.080	3.64	.103	...	...	...	...	...	...	...	...	...

Table 13

Changes in the Ash Content of Fruiting Canes and Laterals, Expressed as Percentage of Dry Weight

	March 27, dormant	May 3, buds starting	June 13, bloom	July 28, fruiting	Aug. 23, after fruiting	Oct. 17, dead
15-inch Canes	1.29	1.45	1.64	1.45	1.51	1.74
Laterals	...	...	5.17	2.54	2.48	2.35
36-inch Canes	1.39	1.45	1.35	1.50	1.31	1.49
Laterals	...	...	5.13	3.46	2.68	2.29
60-inch Canes	1.38	1.51	1.40	1.54	1.40	1.69
Laterals	...	...	4.93	2.77	2.82	2.37
Buds	4.30	2.66	...	...	...	...

CONCLUSIONS

It has been shown that the common food substances generally tend to increase in percentage in direct relation to height of cane and that the moisture content follows the opposite trend. The effect of pruning upon the food substances of the cane appears to have been more a loss of the stored foods in the portions of the canes removed rather than any appreciable change in the behavior of the food substances subsequent to pruning. It is likely that conditions governing the amounts of food substances stored in the canes during the first year of growth have more effect upon these substances than do variations in the subsequent pruning treatment.

The increase in percentage of the carbohydrate materials in the period following fruiting appears to be related to the breakdown of the phloem, which is known to occur at about the same time. As the phloem is intimately concerned with the downward translocation of carbohydrate materials, the disintegration of this tissue at the base of the canes probably brings about the increase of these materials in the canes.

SUMMARY

1. Within recent years a series of related studies have been made dealing with the response of the Latham red raspberry to variations in the severity of spring pruning. In this report consideration is given to the effects of pruning upon growth, and upon the food substances in the cane.
2. Severe pruning tended to increase the relatively small number of new canes or exceptionally vigorous fruiting laterals borne near the base of the canes.
3. Severe pruning tended to increase the relatively small percentage of twin laterals. As a rule, these twin laterals were weaker than nearby solitary ones, indicating that the food reserves available at a given

node may not be sufficient for the normal development of twin laterals.

4. With increasing severity of pruning there was a tendency for a larger number of fruiting laterals to be produced, not only at the base of the canes but at all other heights as well.
5. The data suggest the possibility that severe pruning of the Latham raspberry cane may lead to a reduction in the vigor of the subsequent growth, at least at the base of the cane.
6. It is probable that there is a relation between the increase in the number of laterals resulting from severe pruning and the slight reduction in the average length of these laterals.
7. As several factors are known to affect materially the growth of the raspberry plant, the introduction of the factor of pruning obviously cannot be expected to lead to a clear-cut demonstration of the effects of pruning upon growth response.
8. In the dormant canes, dry matter, reducing sugars, total sugars, total reserve carbohydrates, total organic nitrogen, and ash were found to increase in percentage with increasing height. The percentage of amino nitrogen was not affected by increasing height, and moisture declined in percentage toward the upper portion of the canes.
9. The percentage of moisture in the fruiting cane was found to decline slightly between the dormant stage and the beginning of bud development. It then increased somewhat to reach its highest point at the time of blooming, after which it declined until the death of the cane. Severity of pruning appeared to have only a minor effect upon moisture content.
10. The percentage of total sugars in both canes and laterals was found to decline throughout the season, except for a notable minor rise following the fruiting season. This rise is thought to be associated with the breakdown of the phloem, which occurs at about the same time. Pruning had little effect upon the percentage of total sugars, except that the samples of the 60-inch canes showed slightly greater amounts due to the inclusion of the upper portions of the cane in which the percentage of these food substances is somewhat greater.
11. The behavior of the reducing sugars was found to follow a course very similar to that of the total sugars. Severity of pruning apparently had little effect upon the percentages found.
12. The percentage of "starch" was found to increase slightly between the dormant period and the time of bud development and then declined throughout the season, except for a slight increase following the fruiting season. This slight increase is believed to be related to

phloem breakdown. Severity of pruning apparently had little effect upon the percentage of starch.

13. The percentage of total nitrogen was found to decline more or less regularly from the dormant season until the death of the canes. A slight rise in the percentage found in the laterals following the fruiting season is believed to be associated with phloem breakdown in the canes. The slight increase in the percentage found in the dead canes is believed to be due to translocation downward from the laterals.
14. The percentage of amino nitrogen was very small but increased slightly between the dormant period and the time of bud development. From then to the time of the death of the cane there was a continuous decline. In the laterals the greatest concentration occurred at the time of blooming and was followed by a continuous decline until the canes died.
15. Changes in the percentage of ash were slight and pruning apparently did not affect the quantities of these substances.
16. The effect of pruning appears to have been in the loss of foods stored in the parts removed rather than in changes produced in the occurrence or behavior of the food substances subsequent to pruning.

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